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Context-dependent differences in the functional responses of conspecific native and non-native crayfishes

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Abstract

Invasive species are proliferating globally and cause a range of impacts, necessitating risk assessment and prioritization prior to management action. Experimentally derived estimates of *per capita* effects (e.g. functional responses) have been advocated as predictors of field impacts of potential invaders. However, risk assessments based on estimates from single populations can be misleading if *per capita* effects vary greatly across space and time. Here, we present a large-scale, multi-population comparison of *per capita* effects of the American spinycheek crayfish, *Faxonius* (formerly *Orconectes*) *limosus*—a species with an extensive invasion history in eastern North America and Europe. Functional responses were measured on individuals from six geographically disparate populations of *F. limosus* in its native and invaded ranges on two continents. These revealed inter-population differences in both the maximum feeding rate and functional response type that could not be explained by the biogeographic origin of the population nor by time since the invasion. We propose that other differences in source communities (including the presence of competitors) impose selective pressures for phenotypic traits that result in dissimilar *per capita* effects. We also compared functional responses of the congeners *F. limosus* and *F. virilis* in the presence and absence of potential competitors to examine indirect competitive effects on feeding behaviour. The maximum

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feeding rate of *F. limosus*, but not *F. virilis*, was suppressed in the presence of heterospecific and conspecific competitors, demonstrating how the *per capita* effects of these species can differ across biotic contexts. In the competitor-presence experiments, individuals from the invasive population of *F. limosus* consistently had a higher maximum feeding rate than those of the native *F. virilis*, regardless of treatment. Our results caution against invasion risk assessments that use information from only one (or a few) populations or that do not consider the biotic context of target habitats. We conclude that comparative functional responses offer a rapid assessment tool for invader ecological impacts under context dependencies when multiple populations are analyzed.

Keywords
competition, context dependence, impact, invasive species, maximum feeding rate, risk assessment

Introduction

Invasive species risk assessment is hampered by a lack of quantitative methods for predicting ecological impact (Jeschke et al. 2014). Moreover, predictions are challenged by context-dependent variation in the invader's *per capita* effects and abundance (Ricciardi et al. 2013). Resource consumption is considered a determining factor affecting an invader's success and ecological impact (Catford et al. 2009; Ricciardi et al. 2013), and high-impact invaders appear more efficient at using key resources than their non-invasive counterparts (Carlsson et al. 2004; Rehage et al. 2005; Morrison and Hay 2011; Dick et al. 2013). Therefore, the relationship between an invader's consumption rate and prey density – i.e. its functional response (FR) – has been proposed as a universal measurable trait that predicts key elements of invasibility and impact (Dick et al. 2017a; but see Vonesh et al. 2017 and Dick et al. 2017b). A comparison of FR offers a standardized estimate of the *per capita* effect (e.g. maximum feeding rate) of study populations to help explain and predict differences in impacts across populations, species, and environment contexts (Haddaway et al. 2012; Dick et al. 2013; Alexander et al. 2014; Barrios-O'Neill et al. 2014; Iacarella et al. 2015a, 2015b). Further information is derived from the shape of plotted FR data, most often characterized by so-called Type II or Type III curves, which indicate whether the predator-prey dynamic is likely to be destabilizing or stabilizing, respectively (Alexander et al. 2012; Dick et al. 2013); Type I curves are mainly observed in filter feeders and rarely in other consumers, as such a relationship only exists when handling does not interfere with searching for resources such as prey (Holling 1959; Jeschke et al. 2014). Previous experiments using a comparative FR approach have demonstrated higher *per capita* effects for invaders compared to trophically or taxonomically similar native or non-invasive species and were also able to predict impacts on prey populations observed in the field (Dick et al. 2013; Alexander et al. 2014).

Few studies have tested whether *per capita* effects are conserved across populations of congeners or conspecifics (e.g. Boets et al. 2019; see review by Jeschke et al. 2014). Although conspecific individuals share traits that contribute to their success and impact as invaders, population traits could differentiate after periods of isolation and, as

a result, produce different impacts (Tsutsui et al. 2003; Dlugosch and Parker 2008; Vellend et al. 2009; Lockwood et al. 2013; Evangelista et al. 2019). Important insights into such variation can be derived from distributed experiments, in which standardized, controlled protocols are employed across a wide geographic range (Fraser et al. 2013; Borer et al. 2014). For example, a study by Dick et al. (2013) examined the FR of invasive bloody red mysid shrimp (*Hemimysis anomala*) in invaded ranges in Quebec and Northern Ireland. While the invader's *per capita* effects were consistently greater than native mysids, they differed between study populations (maximum feeding rate of 1.82 *Daphnia pulex*/hour in Northern Ireland versus 3.39 *D. pulex*/hour in Quebec) (Dick et al. 2013), possibly reflecting differences in experimental handling, animal care, or population traits. This finding raises the question of how variable FR is across conspecific populations and ecological contexts. It has been hypothesized that sources of variation in *per capita* effects include biogeographic (native/non-native) origin (Rehage et al. 2005; Paolucci et al. 2013), time since invasion (Iacarella et al. 2015a, 2015c; Evangelista et al. 2019), and community structure (Hayes et al. 2009).

Here, in two sets of experiments we measured the *per capita* effects of the American spinycheek crayfish *Faxonius* (formerly *Orconectes*) *limosus* and the virile crayfish *F. virilis*, both of which have extensive invasion histories (Henttonen and Huner 1999; Souty-Grosset et al. 2006; Taylor et al. 2007) but are also threatened in parts of their native ranges by introduced congeners (Dubé and Desroches 2007; Swecker et al. 2010). We compared the FR of geographically disparate populations of *F. limosus* in its native and invaded ranges. To assess the role of biotic context in mediating impacts, we also compared the maximum feeding rates of *F. limosus* and *F. virilis* in the presence of heterospecific and conspecific competitor signals. We predicted that the FR (curve type and maximum feeding rates) would differ significantly between conspecific populations of *F. limosus*, owing to divergence of population traits. Additionally, we tested the hypothesis that invasive populations have a greater maximum feeding rate, and thus impact (Dick et al. 2013), based on the premise that crayfish have increased growth rates – and thus greater energetic demands – in their invaded range than native conspecifics (Pintor and Sih 2009; Sargent and Lodge 2014). Finally, we predicted that the *per capita* effects would be reduced in the presence of a perceived competitor, owing to feeding activity being inhibited by agonistic interactions.

Methods

Animal collection and care

Experiments were conducted in climate-controlled facilities at Queens University Belfast (UK) and McGill University (Canada) to ensure environmental conditions were constant throughout trials. In the summers of 2016 and 2017, *F. limosus* were collected from two native populations (hereafter designated by *N*; Quinebaug River, Massachusetts: 42°06'32"N, 72°07'25"W; Panther Pond, Maine: 43°54'04"N, 70°27'55"W)

and four invasive populations (hereafter designated by *I*; St Lawrence River, Quebec: 46°09'22.81"N, 72°59'54.85"W; St Croix River, New Brunswick: 45°37'01"N, 67°25'35"W; Lake Müggelsee, Germany: 52°26'54"N, 13°38'55"E; Albert Canal, Belgium: 50°56'34"N, 5°29'27"E). Crayfish collected from European sites were transported overnight by courier to Queen's University Belfast. North American populations were transported by research vehicle from the field site to McGill University within 2–48 h of collection. The population of *F. limosus* from the St Lawrence River (*I*) was used first in distributed experiments and then in competitor-signal experiments three months later. Individuals of *F. virilis* used in competitor-signal experiments were collected from Blue Chalk Lake (*N*) in Dorset, Ontario (45°11'55"N, 78°56'20"W). For competitor-signal experiments, subjects were held in communal aquaria with up to five other individuals for three months prior to experiments. All crayfish collected from their invasive range were done so in areas where no other crayfish species currently co-exist. In contrast, those collected in their native ranges were from sites with sympatric crayfish species.

Crayfish were introduced to holding tanks at 18 °C immediately upon arrival and allowed to acclimate for at least one week prior to the start of experiments. Individuals were housed at low densities with ample shelter to mitigate territorial and aggressive behaviour (Reynolds et al. 2013) and they were fed a diet of sinking shrimp pellets. Aquaria maintenance included weekly water changes (25–50%, depending on tank size and crayfish density) and biweekly water quality testing. Given that *Faxonius* spp. are more active at night (personal observation), experimental animals were acclimated to a reversal of their usual 12:12 hour light:dark regime over a period of 96 h, following Alexander et al. (2012).

Low sample sizes of *F. limosus* obtained in the St Lawrence River (*I*) required that some individuals from this population be used in more than one trial, but each individual was tested only once at each density and in a maximum of three trials. To track individual identity, each crayfish was tagged with visible implant elastomer tags – a method that has been shown to have high tag retention rates and no influence on crayfish growth rates or mortality (Clark and Kershner 2006; Buřič et al. 2008).

Experimental designs

Distributed experiments

All experiments were completed by the same researcher to minimize handler variation that often occurs in spatially distributed experiments coordinated among multiple research groups (Fraser et al. 2013; Dick et al. 2013). FR trials were conducted at ambient temperatures of 18 °C in opaque experimental tanks (61 cm × 35.5 cm filled with 10.8 L of water, and no substrate), and provided with a single PVC pipe as shelter (~12 cm length, 5 cm diameter). Experiments allowed for prey depletion, potentially underestimating the attack rate. However, the type of FR curve, handling time and maximum feeding rates remain uninfluenced by this procedure (Alexander et al. 2012).

Owing to natural variation in body size (carapace length) among populations of *F. limosus* crayfish and the low sample sizes available, no attempt was made to size-match individuals; instead, crayfish representing the estimated median size of individuals within each source population were used (see Suppl. material 1). Crayfish were introduced into experimental tanks 24 h prior to the beginning of experiments and were not fed during this period to standardize hunger levels. Following acclimation, each individual was randomly assigned one of 11 prey density treatments (3, 4, 5, 7, 10, 15, 20, 25, 30, 40 or 50 gammarid amphipod individuals of *Gammarus pulex* in the UK and *Gammarus fasciatus* in North America). In addition, one control treatment at each prey density was conducted in the absence of a crayfish to account for potential mechanisms of prey death other than crayfish predation. Experiments were run for 6 h in the dark, after which the crayfish were removed from experimental tanks and the remaining gammarids counted to determine the number of prey consumed. This procedure was replicated three times for each crayfish population (n = 33, plus controls for each population). Following each trial, crayfish were blot-dried and weighed, and their carapace length was measured.

Amphipod prey activity levels

We did not have access to a gammarid prey species common to both the UK and eastern North America (NA); therefore, it was necessary to account for differences in body size (length) and activity levels of a subsample (n = 30) of *Gammarus* spp. from each region. Activity level was measured at 18 °C by placing an individual amphipod into a petri dish filled with 1 cm of dechlorinated tap water, allowing the individual to acclimate for 90 s, and then counting the number of times it crossed the center of the dish in 60 s (Maynard et al. 1998).

Competitor-signal experiments

This second set of FR experiments took place between February 10 and April 18, 2017, and consisted of six experimental treatments using the two crayfish species in a full factorial design, plus predator-free controls (Table 2). Experiments featured 'focal' and 'competitor' crayfish(es) that occupied a shared experimental arena but had minimal physical contact. Experimental conditions were identical to those of the distributed FR experiments, except that the addition of a lidded container with 1cm holes in each side was included in the experimental arena. The focal crayfish wandered freely in the experimental chamber and could access the shelter, while the competitor crayfish was confined to the secondary container. The container holes were large enough to allow crayfish antennae and claws to pass through, but the competitor was unable to access the prey.

The focal and competitor crayfish were introduced to the experimental chamber simultaneously, 24 h before the beginning of the trial. The beginning of the trial was signalled by the introduction of defrosted bloodworms (Diptera, Chironomidae, *Chironomus*) to the experimental chamber, in each of the following prey densities: 15, 20, 25, 30, 40, 50, 60, 70, 80, 100, and 120 individuals. Trials lasted 6 h in the dark and allowed for prey depletion. Each of the 11 densities in each treatment was replicated in triplicate (n = 33 for

each of the six experimental treatments, plus one replicate at each density as a predator-free control). After each trial, crayfish were blot-dried and weighed, and their carapace length measured. The remaining prey were counted to determine the number attacked during the trial. Prey were scored as 'attacked' if at least part of the worm had been eaten (determined by fragmented worms and loss of colour caused by draining of hemolymph). Owing to insufficient numbers of experimental animals, individual crayfish were re-used in trials up to 10 times, but never re-used twice at the same density, regardless of treatment.

Statistical analysis

Model selection and fitting

All analyses were completed using R (version 3.2.4). As is appropriate for prey non-replacement designs, FR was modeled using the Random Predator Equation (Rogers 1972) for Type II curves and Hassell's equation (Hassell et al. 1977) for Type III curves, following Alexander et al. (2012) and Iacarella et al. (2015a). Model selection was conducted using three methods outlined by Pritchard et al. (2017). The best fit model was selected for each population (distributed experiments) and experimental treatment (competitor-signal experiments), based on consensus of selection methods. Best-fit models were fit to FR data via maximum likelihood estimation (see Suppl. material 2).

Model comparisons

To compare the fitted FR curves among populations and experimental treatments, the data were bootstrapped (n = 999) to produce 95% confidence intervals (CI) on the fit. Using this method, we may statistically compare models between populations by simply observing the overlap, or lack of, between model CIs (Pritchard et al. 2017). In addition, the *frair_compare* function of the FRAIR package was used to compare the difference in handling time (h) estimates between populations, but is limited to comparing those that are fit by the same model type (Pritchard et al. 2017). An overall assessment of differences between model parameters can also be achieved by observing overlap between 95% CIs, as with full model comparisons. The effect of crayfish size (carapace length and weight) on maximum feeding rate and proportion of prey killed was tested using linear models (linear regression for each population). Sex-related effects were also assessed for each population using t-tests to compare the proportion of prey consumed between sexes.

Results

Distributed experiments

Functional responses differed among populations by maximum feeding rate and curve type. The responses of populations from Lake Müggelsee (I), Albert Canal (I), and the

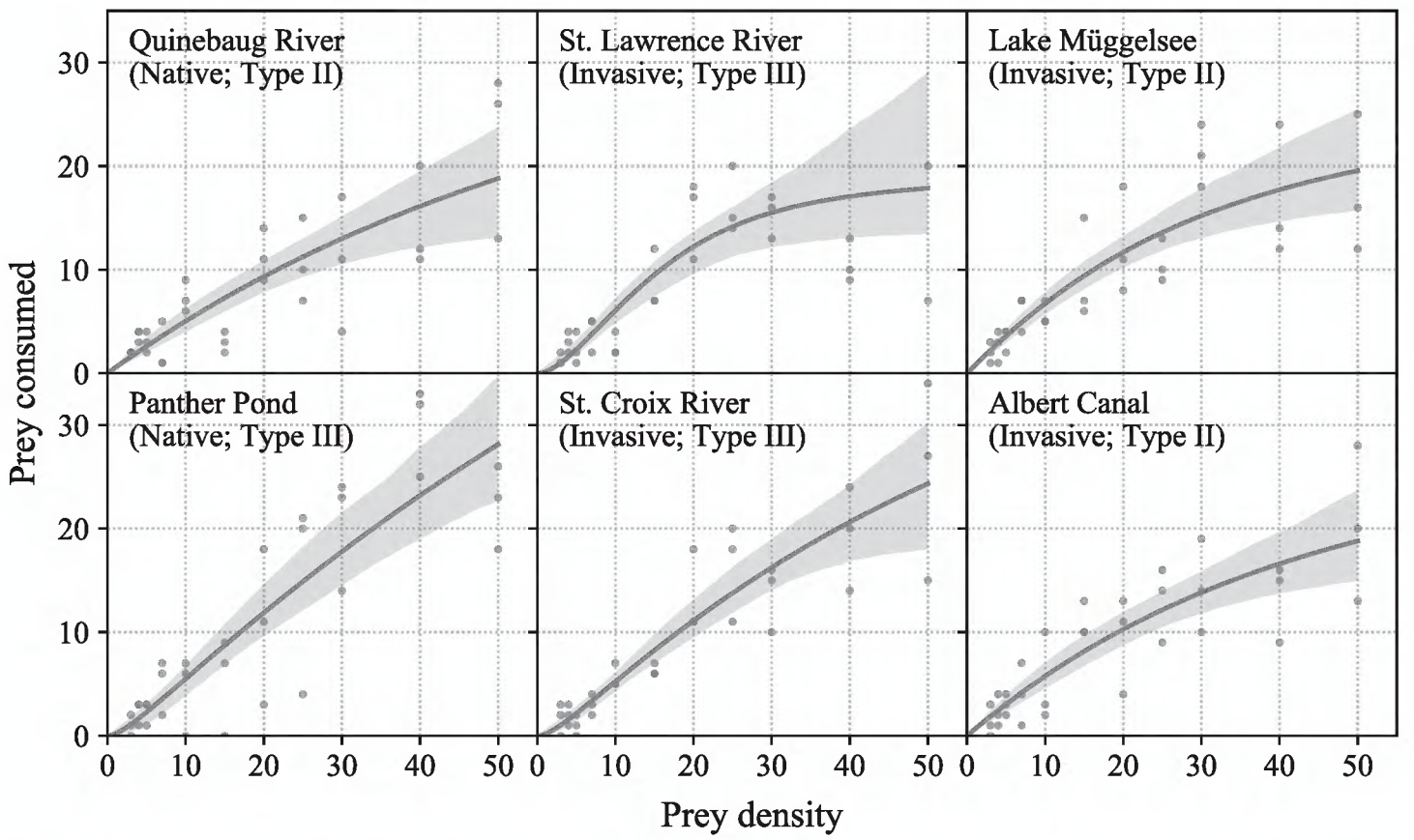

Figure 1. Functional response curves with bootstrapped 95% confidence intervals (shaded regions) for *F. limosus* from native and invasive populations. Lines represent the best fit model for each population (Type II or Type III). n = 33 for each population.

Table 1. **(a)** Comparisons between handling time (h) parameters for populations fit with Type II curves. Δh represents the difference (Δ) in h between the two populations' model fits. (*) represents a significant difference to the standard α = 0.05. **(b)** Comparison between h parameters for populations fit with Type III curves.

	Fit 1	Fit 2	Δh (h)	p-value
(a)	Lake Müggelsee (*I*)	Albert Canal (*I*)	0.016	0.76
	Lake Müggelsee (*I*)	St. Croix River (*I*)	0.17	0.0012*
	Lake Müggelsee (*I*)	Quinebaug River (*N*)	0.075	0.24
	Albert Canal (*I*)	St. Croix River (*I*)	0.15	0.0087*
	Albert Canal (*I*)	Quinebaug River (*N*)	0.058	0.39
	St. Croix River (*I*)	Quinebaug River (*N*)	-0.096	0.16
(b)	St. Lawrence River (*I*)	Panther Pond (*N*)	0.21	0.02*

Quinebaug River (*N*) were best fitted by a Type II curve, while those of remaining populations were best fitted by a Type III curve (Fig. 1). Bootstrapped 95% confidence intervals indicated significant overlap in model fits and maximum feeding rates among the populations, regardless of whether the population was native or invasive (Fig. 1); however, parameter comparisons using the *frair_compare* function indicate a significantly greater maximum feeding rate (lower handling time, h) for the population of *F. limosus* from the St Croix River (*I*) than either the Lake Müggelsee (*I*) or Albert Canal (*I*) populations. Similarly, the Panther Pond (*N*) population exhibited a greater maximum feeding rate than the St Lawrence River (*I*) population (Table 1).

Crayfish predation was the principal source of prey death in experimental trials, as indicated by high survival rates in control treatments (across all populations, controls exhibited

Table 2. Treatments for functional response experiments in which the focal crayfish was allowed to roam freely in the experimental chamber with access to prey and shelter, while the perceived competitor crayfish was confined to a porous container within the experimental chamber. L = *F. limosus* alone, LL= *F. limosus* with an *F. limosus* competitor, LV = *F. limosus* with an *F. virilis* competitor, V = *F. virilis* alone, VL= *F. virilis* with an *F. limosus* competitor, and VV = *F. virilis* with an *F. virilis* competitor. Sample size, n = 33 in the first six experimental treatments and n = 11 for the control treatment.

Treatment	Focal species	Competitor species
V	*F. virilis*	–
L	*F. limosus*	–
VV	*F. virilis*	*F. virilis*
LL	*F. limosus*	*F. limosus*
LV	*F. limosus*	*F. virilis*
VL	*F. virilis*	*F. limosus*
Control	–	–

99.98% survival of prey during 6-hour experimental trials). Overall, maximum feeding rates declined with mean crayfish size and weight (linear models; carapace length: $F_{1,4}$ = 10.83, p = 0.030, weight: $F_{1,4}$= 10.40, p = 0.032), but the size effects on prey consumption varied among populations. The proportion of prey consumed increased with crayfish size for the Panther Pond population (*N*) (linear models; carapace length: $F_{1,31}$ = 4.36, p=0.048, adjusted r^2 = 0.09, weight: $F_{1,31}$ = 6.91, p = 0.013, adjusted r^2 = 0.16), but decreased with crayfish weight for the Albert Canal population (*I*) (linear model; $F_{1,31}$ = 4.68, p = 0.038, adjusted r^2 = 0.10). Female crayfish from the Quinebaug River population consumed a marginally greater proportion of prey (*t*-test; t_{28} = 2.45, p = 0.021) than males. No differences in prey consumption were detected between crayfish sexes in other populations.

Amphipod prey activity levels

Amphipods used as prey in FR experiments in the UK (*G. pulex*; mean size ± SE = 6.67 mm ± 0.50) and North America (*G. fasciatus*; 6.10 mm ± 0.48) did not differ in size (Mann-Whitney U Test; W = 560.5, p = 0.091). However, North American prey were significantly more active than UK prey, crossing the centre of the disk an average of 5.7 times per minute (SE = 1.8) while *G. pulex* in the UK crossed an average of 3.7 times per minute (SE = 1.1) (Mann-Whitney U Test; W= 624, p = 0.0098).

Competitor-signal experiments

The maximum feeding rate of *F. limosus* was suppressed in the presence of conspecific and heterospecific competitors, whereas the handling time (and thus, maximum feeding rate) of *F. virilis* was unaffected (Fig. 2, Table 3). However, despite apparent inhibition in the presence of competitors, *F. limosus* consistently exhibited a significantly higher maximum feeding rate than that of *F. virilis* (Fig. 2). All treatments were best fitted by Type II curves.

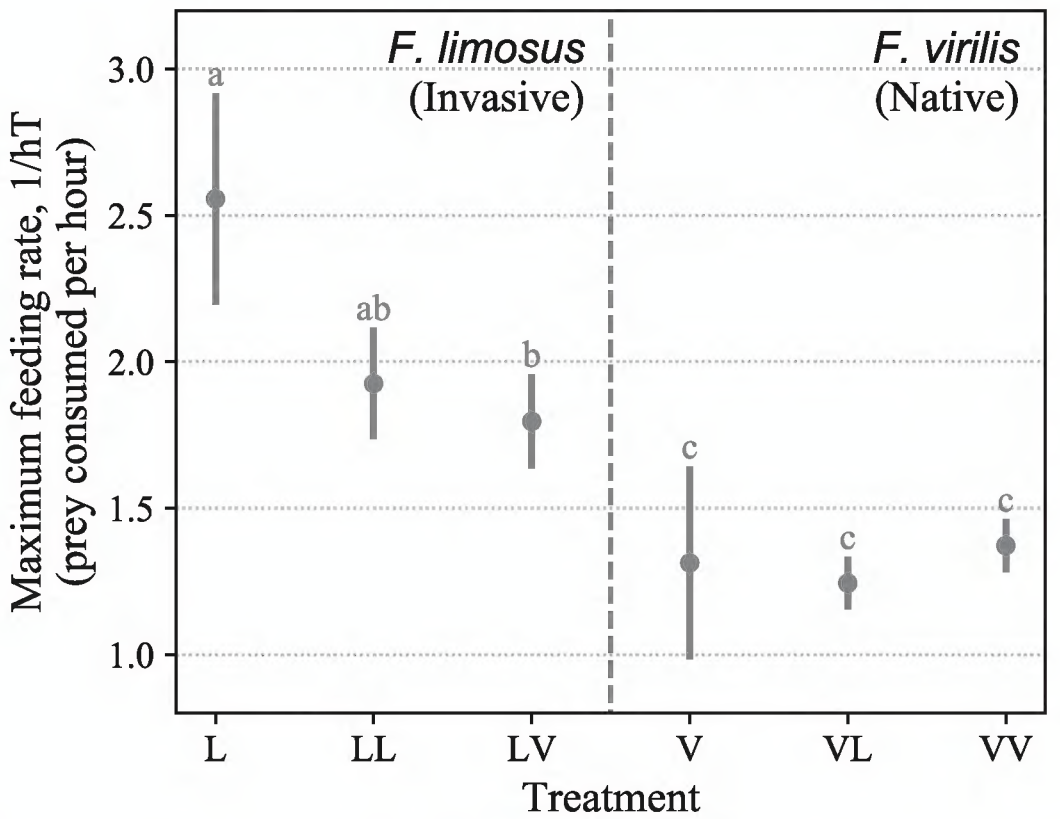

Figure 2. Maximum feeding rate (MFR) calculated for each treatment in the competitor-signal experiments ($1/hT$, where h is estimated handling time and T is experimental duration). Treatment codes represent the focal and competitor crayfish species in each treatment – L = *F. limosus* alone, LL = *F. limosus* with an *F. limosus* competitor, LV = *F. limosus* with an *F. virilis* competitor, V = *F. virilis* alone, VL = *F. virilis* with an *F. limosus* competitor, and VV = *F. virilis* with an *F. virilis* competitor. *F. limosus* used in these experiments came from an invasive population, whereas *F. virilis* came from a native population. Bars indicate the standard errors of the MFR calculated by propagating the model fit standard error given for h for each treatment. Differences in letters above error bars indicate significant differences ($\alpha = 0.05$) between treatments. $n = 33$ for each treatment.

Table 3. Comparisons between handling time (h) parameters for populations fit with Type II curves. Δh represents the difference (Δ) in h between the two treatments' model fits. (*) represents a significant difference to the standard $\alpha = 0.05$.

Fit 1	Fit 2	Δh (h)	p-value
L	VV	0.012	< 0.0001*
L	VL	-0.069	< 0.0001*
V	L	0.062	0.00024*
LL	VL	-0.048	0.00038*
VL	LV	0.041	0.0015*
VV	LL	0.035	0.0028*
VV	LV	0.029	0.011*
V	LL	0.040	0.015*
L	LV	-0.028	0.025*
V	LV	0.034	0.036*
L	LL	-0.021	0.095
VV	VL	-0.013	0.32
LL	LV	-0.0063	0.60
V	VL	-0.0072	0.68
V	VV	0.0054	0.74

Despite significant size differences between *F. limosus* and *F. virilis*, carapace length and crayfish weight were not significant predictors of maximum feeding rate (linear models; carapace length: $F_{1,4} = 0.055$, $p = 0.83$; weight: $F_{1,4} = 0.059$, $p = 0.82$).

Discussion

Our study demonstrates intraspecific variation in the *per capita* effects of conspecific populations. The *per capita* effects of *Faxonius* crayfishes differed across geographically disparate populations and different biotic contexts. Despite large confidence intervals on model fits, we detected differences in both FR curve type and maximum feeding rates between conspecific populations of *F. limosus* (Fig. 1, Table 1). The source of differences remains to be determined, but we are confident that it is not an artifact of our experimental design, because in addition to the implementation of standardized protocols and controls in experimental procedures, handler variation was minimized by having the same individual researcher responsible for all animal care and experiments. In addition, crayfish were selected to represent the median population size and therefore representative of true population differences. Nevertheless, there was no consistent relationship between crayfish body size and maximum feeding rates, nor between crayfish sex and the proportion of prey consumed. Finally, differences in amphipod activity level did not explain variation in maximum feeding rates, as demonstrated by remarkably similar maximum feeding rates found between the European (*I*) and St Lawrence River (*I*) populations which were supplied different gammarid prey species. The most discordant maximum feeding rates were amongst populations within North America, which were supplied with a common prey species.

Our prediction that invasive populations of *F. limosus* would have greater maximum feeding rates than native populations was not supported, perhaps owing to an insufficient number of populations studied. There are numerous potential explanations for differences among *per capita* effects of populations, including differences in resident community composition (Barrios-O'Neill et al. 2014; Médoc et al. 2015; Wasserman et al. 2016), time since invasion (Iacarella et al. 2015a, 2015c; Yokomizo et al. 2017; Evangelista et al. 2019) and abiotic conditions (Eggleston 1990; Alexander et al. 2012; Iacarella et al. 2015b), but we were unable to determine the cause in our distributed experiments. In mesocosm experiments, Evangelista et al. (2019) found contrasting ecological impacts amongst individuals from four invasive populations of red swamp crayfish (*Procambarus clarkii*) and thus demonstrated that even geographically-close populations can vary in intraspecific trait variability, consistent with studies showing trait differences amongst individuals across a single expanding population (e.g. Iacarella et al. 2015a). They found that crayfish from the most recently invaded lakes in their study had the greatest impacts on ecosystem processes.

Our populations were sourced from locations with differing biotic contexts: all invasive populations from Europe and Canada were collected from sites where no other crayfish species were detected, whereas native populations collected from the USA were

found in sympatry with congeners. Hayes et al. (2009) demonstrated that *F. virilis* from populations sympatric with *F. rusticus* (30 years of coexistence) grew faster and were more aggressive towards the congener than naïve populations of *F virilis*. Conversely, Pintor et al. (2008) found that invaders from sites without a congeneric competitor were bolder, more voracious and more aggressive towards congeners relative to those from sites with competitor crayfish; they postulated that this trend was due to differences in prey densities between sample sites, with more aggressive crayfish hailing from low prey density sites. However, trends in our data could not be explained by sympatry with congeners and, owing to the correlation of biotic context and invasive status (all invasive populations were allopatric to other crayfish species) in our study, we are unable to disentangle possible effects. Increasing the scope of conspecific populations studied should allow for more power to test for hypothesized trends and improve predictions.

Biotic context mediates *per capita* effects

Our competitor-signal experiments tested the influence of biotic context on *per capita* effects of invasive species and found that closely related species differ in their response to the presence of competitor signals. Invasive *F. limosus* adjusted its feeding behaviour in the presence of conspecific and heterospecific competitor signals, whereas native *F. virilis* did not (Fig. 2). However, even where the maximum feeding rate of *F. limosus* is suppressed, it still exceeds that of the native, consistent with the resource consumption hypothesis (Dick et al. 2013; Ricciardi et al. 2013). This result suggests that *F. limosus* can have a greater impact on prey populations than *F. virilis* where the two species are sympatric; but as demonstrated, impact differs between *F. limosus* populations. Therefore, conclusions on the potential species impacts cannot be reliably drawn from estimates from only one population. We tested individuals from a population of *F. virilis* that was sympatric with a native congener (*F. propinquus*), whereas our *F. limosus* population was allopatric. We hypothesize that the suppression of feeding rates resulted from intimidation by adversarial crayfish, the effect of which could dampen over time as dominance hierarchies are established and agonistic interactions decline (Goessmann et al. 2000). Thus, a likely explanation for the unaffected feeding rate of *F. virilis* in the presence of a competitor is that individuals from this population are accustomed to the presence of other crayfishes.

For *F. limosus*, the presence of congeners can trigger individuals to trade off foraging effort with shelter protection. Access to suitable shelters is crucial for crayfish survival by enhancing predator avoidance, facilitating successful moulting, and reducing the frequency and intensity of agnostic interactions with other individuals (Nyström 2005, Hirsh et al. 2016, Lele and Pârvulescu 2017). Previous studies have demonstrated the superior ability of invasive crayfishes to evict natives and co-opt shelters for themselves (Lele and Pârvulescu 2017), aided by increased aggression (Klocker and Strayer 2004). Therefore, a reduced maximum feeding rate could have been the result of *F. limosus* sacrificing foraging opportunities to maintain possession of shelter in the presence of a perceived competitor. A competitor signal might have triggered increased aggressive or territorial behaviour in

F. limosus at the expense of sacrificing its foraging effort. We did not make observations throughout the trial and so cannot confirm these behaviours. In contrast, the lack of a behavioural change in *F. virilis* in the presence of competitors might also be explained by shelter usage; Garvey et al. (1994) examined interspecific competition for shelter among congeneric *Faxonius* crayfishes and determined that among the three species studied, *F. virilis* was most often found actively mobile outside of shelters even in the presence of predators. Bold behaviour and naivety to competition from non-native species could prevent crayfishes from trading off feeding intensity for shelter or territorial protection.

Conclusions

We conclude that *per capita* effects, and thus possibly overall field impacts, of crayfishes are mediated by context dependencies including indirect species interactions. Although we were unable to detect trends explaining the sources of variation in our distributed experiments, the observed differences in *per capita* effects indicate the need to conduct broader comparisons of conspecific populations separated by a range of geographic distances, in order to test the generality of hypotheses related to invasion impact (Ricciardi et al. 2013). We advocate the development and testing of hypotheses that explicitly incorporate context dependencies from both the source and recipient communities of invasive species.

Crayfish populations are declining worldwide; nearly half of all species in North America are considered endangered or vulnerable (Taylor et al. 2007), owing in part to the spread of invasive species (Crandall and Buhay 2008). Those in the genus *Faxonius* (formerly *Orconectes*) are not exempt from this trend, but remarkably are also among the most disruptive invaders. Our results suggest a mechanism (feeding efficiency) by which the success and impact of these crayfishes vary with different environmental contexts. Understanding the causes of variation in their *per capita* effects would not only inform the prioritization and management of invasive populations but could also be valuable to the conservation of threatened populations. Most risk assessments of invader impact rely upon either expert opinion or invasion history (Ricciardi 2003; Kulhanek et al. 2011; Dick et al. 2013), whereas comparative experimental approaches that consider both species traits and environmental context offer standardized, objective, and informative measures of *per capita* effects that could be used in prioritizing emerging and potential future invaders. However, our results caution against deriving risk assessment information from studies of a single population.

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Supplementary material 1

Crayfish size and weight

Authors: Jaime Grimm, Jaimie T.A. Dick, Hugo Verreycken, Jonathan M. Jeschke, Stefan Linzmaier, Anthony Ricciardi

Data type: measurement

Explanation note: Body weights and carapace lengths of individuals.

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Link: https://doi.org/10.3897/neobiota.54.38668.suppl1

Supplementary material 2

Statistical techniques

Authors: Jaime Grimm, Jaimie T.A. Dick, Hugo Verreycken, Jonathan M. Jeschke, Stefan Linzmaier, Anthony Ricciardi

Data type: statistical data

Explanation note: Details of statistical methods.

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Link: https://doi.org/10.3897/neobiota.54.38668.suppl2

Supplementary material 3

Locations of crayfish populations

Authors: Jaime Grimm, Jaimie T.A. Dick, Hugo Verreycken, Jonathan M. Jeschke, Stefan Linzmaier, Anthony Ricciardi

Data type: occurrence

Explanation note: Geographical coordinates of populations.

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Supplementary material 4

Amphipod sizes

Authors: Jaime Grimm, Jaimie T.A. Dick, Hugo Verreycken, Jonathan M. Jeschke, Stefan Linzmaier, Anthony Ricciardi

Data type: measurement

Explanation note: Body lengths of amphipod prey used in the experiments.

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Link: https://doi.org/10.3897/neobiota.54.38668.suppl4

Supplementary material 5

Data from functional response experiments

Authors: Jaime Grimm, Jaimie T.A. Dick, Hugo Verreycken, Jonathan M. Jeschke, Stefan Linzmaier, Anthony Ricciardi

Data type: measurement

Explanation note: Functional response parameters from experimental trials.

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